THE LUMINOUS ORGAN OF THE NEW ZEALAND GLOW-WORM.[1]

By W. M. Wheeler and F. X. Williams.

The earliest description of the New Zealand glow-worm seems to be given in a brief note by Meyrick published in the *Entomologists' Monthly Magazine* for 1886. This observer found a number of larvæ, which he supposed to be those of a Staphylinid beetle, on the damp, precipitous banks of a densely shaded creek near Auckland. The larvæ were described as burrowing "in the earth, exposing the head and anterior portions from the burrow but having in front of them a sort of irregular slimy network." They occurred in such numbers that more than fifty were counted in a square foot of surface. Meyrick states that the same or a similar species has been noticed in caves and mines in other parts of New Zealand. He says that "the light consists of a small light-greenish white erect flame rising from the back of the neck," and that the food of the creature consists of minute insects probably attracted by its light.

During 1886 and 1887 Hudson published accounts of the insect and pointed out several errors in Meyrick's description. He showed that the luminous larva is not so numerous in a given area, that its light does not proceed from the neck but from a large glutinous knob at the posterior end of the body and that it inhabits irregular cavities in the earthen banks "where it hangs suspended in a glutinous web, which also appears to envelop the body, large quantities of sticky mucous being periodically shot out of the mouth of the larva and formed into threads as required." Hudson supposes that the larva feeds on decaying vegetable matter. He saw the light displayed most brilliantly at 3 or 4 o'clock in the morning but on several occasions observed no light all the evening. The light does not serve to attract food but "to assist the larvæ in escaping from enemies, as when disturbed they nearly always gleam very brilliantly for a few seconds, suddenly shutting off the light and retreating into the earth." The ¡mago reared in the breeding cage proved to be a Tipulid fly which

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was identified as *Trimicra pillipes* by Baron Osten-Sacken. The noted dipterist, however, regarded the luminous larvæ sent to him as those of a Mycetophilid (1886).

A more exhaustive account of the life-history of the New Zealand glow-worm was published by Hudson in 1891. He studied the insect in the deep ravine of the botanical garden at Wellington and with some difficulty worked out its transformations. It proved to be a Mycetophilid and was described by Skuse as *Bolitophila luminosa* in an appendix to Hudson's paper. The imago, identified by Osten-Sacken as *Trimicra pallipes* did not, therefore, develop from one of the luminous larvæ but from another larva that had accidentally entered Hudson's breeding cage. The pupa of the *Bolitophila* is figured with a large branched and apparently tracheal process on the prothorax. The anal segment was found to be luminous in life and the imaginal flies, all of which proved to be females, were also luminous, emitting from the tip of the abdomen "a strong light about half as bright as that emitted by a full grown larva."

On September 5, 1914, the senior author, while visiting New Zealand, took part, through the kindness of Mr. T. F. Cheeseman, in an excursion to the Waitakari Forest, near Auckland, for the purpose of inspecting some of the few large surviving kaori-pines (*Agathis australis* Salisb.). In order to reach the forest by a short cut it was found convenient to traverse a dark tunnel many yards in length excavated through a small mountain and serving as a viaduct for a pipe from a large reservoir to the water-works of the city of Auckland. The walls of this tunnel were spangled with beautiful blue-green sparks, which proved, on examination, to be the luminous *Bolitophila* larvæ described by Hudson. They varied from about 1 to 3.5 cm. in length and were living on slender glutinous threads which, in some cases, depended from the ceiling of the tunnel. Several of them, transferred to a moist vial, were later examined under a strong pocket lens and showed the luminous organ very distinctly in the dilated ovoidal terminal segment of the body. This segment bears a pair of small, jointed cerci and is, therefore, probably the eleventh abdominal metamere. The organ appeared as four parallel rods closely applied to one another in the middle of the vesicle on the ventral surface of the very slender rectum. Their long axes were parallel with the long axis of the body and all were slightly curved, so that the oblong plate which they formed together was concave on the dorsal and convex on the ventral surface. They gave off a bluish-green light most intensely from their dorsal surfaces, as their ventral surfaces appeared to be covered with a vague mass of reflecting tissue.

The specimens were killed in 50 per cent. and then transferred to 70 per cent. alcohol, which seemed to preserve them sufficiently well for subsequent study. The junior author sectioned a number of the specimens and stained them with Heidenhain's iron hæmatoxylin. He also obtained excellent views of the structures as whole mounts or partial dissections stained in alum cochineal.

Fig. 1, Pl. 3, represents one of the larvæ in lateral view. The head is very small, with minute eyes; the long body grows broader posteriorly and terminates in a bulbous enlargement or vesicle, separated by a distinctly constricted region from the more anterior segments. If this constricted region is counted as a segment the abdomen has the full number, eleven, of segments characteristic of insects. Hudson's figure of the larva (Pl. 8, Fig. 1) is certainly incorrect, since it represents no less than nineteen post-thoracic segments and the outline of the terminal bulbous segment is defective. It is probable that this region in our figure is too small, as it was drawn from a preserved and perhaps somewhat shrunken specimen.

The peculiar glutinous web on which the larva moves about is evidently secreted by a pair of voluminous spinning glands situated in the anterior two thirds of the body. Their posterior tips are represented at SG in Fig. 2, which is drawn from a dissection of the slender hind-gut and the accompanying Malpighian tubules in the posterior third of the body as seen from the ventral side. These Malpighian tubules are four in number as in other Diptera and all come off at the same level, run forward a short distance and then turn back with more or less convolution, applying themselves to the sides of the slender intestine. They gradually diminish in diameter till they become very tenuous and straight in the constricted region just anterior to the terminal vesicle and are there closely applied to one another side by side on the ventral surface of the rectum. Then they separate along the median line into two pairs and again come together but increase two and one-half to three times in diameter in the vesicle where they terminate with rounded tips. It is these dilated tips of the four Malpighian tubules which appear as the four curved, luminous rods in the living larva and, therefore, constitute the photogenetic organ. What to all appearances serves as a reflector is represented by a layer of tissue (R, Figs. 3 and 7) of variable thickness, covering much and in life perhaps all the ventral surface of the dilated ends of the tubules. A pair of large tracheæ, shown at T, enters this layer and each breaks up almost immediately into three branches, one of which runs back between each of the two pairs of Malpighian tubules. The reflecting layer seems to be a syncytium made up of the hypertrophied and finely vacuolated tracheal epithelium, as it reveals no cell boundaries. It contains numerous small nuclei which are all at one level well within the mass (Fig. 7) and close to the chitinous tracheal intima. Anteriorly the reflecting layer extends for a short distance along the two main tracheal trunks, but posteriorly it thins out into a membrane which partly serves to secure the tubules to the rectum. Some slender longitudinal muscles, shown at M in Fig. 3, have the same function. It is probable that the reflecting syncytium may in life contain numerous fine vacuoles of a fatty substance which has been dissolved away in the mounted preparations. We do not believe that this layer is derived from the fat-body, because the latter, as shown in Fig. 5, consists of larger cells with definite boundaries and large, spherical nuclei.

It thus appears from dissection that the Malpighian tubules are each differentiated into two portions with very different functions, viz., a short distal piece which is photogenetic and a long proximal portion which retains the primitive excretory function of these organs. The portion anterior to the subterminal constriction of the body shows in both stained and unstained material a more opaque and vacuolated structure of its cells, with darker nuclei; the slender intermediate region (Fig. 2S) is much more transparent and its nuclei are paler, while the photogenetic portion is also rather pale but consists of much larger cells. In sections these structural differences are even more marked. No sections were taken near the points of origin of the Malpighian tubules, but it is evident from a specimen stained *in toto* that the lumen is here quite large. A section through the middle region is shown in the lower of the two drawings in Fig. 4. The wall of the tubule shows only two cells, both so much swollen as to reduce the lumen to a mere line, except at one side where the wall is reduced to a mere membrane bounding a small passage. The canal may be even more reduced than in the section figured, but it is commonly slit-like and was never seen to be large and circular in this region. The cells are vacuolated and contain some darkly staining granules. A section through the intermediate narrow portion of the tubule just in front of the photogenetic region and corresponding with the point S in Fig. 2 is shown in the upper drawing of Fig. 4. The lumen, though similar to that in the anterior region, is more evident. The cell content is denser and more granular and approaches that of the cells in the luminous organ. All four tubules of this latter region are shown in cross-section in Fig. 7. They are circular, with large lumina, and the walls consist of four well-defined cells, with large spherical nuclei. Their cytoplasm is throughout densely packed with minute granules which stain very deeply, so that the tubules stand out in marked contrast with the underlying reflecting layer. Evidently these granules correspond in function with the photogenetic granules in the luminous organ of the fire-fly. Vacuoles are rare or altogether lacking in these cells, as in the section figured. The lumina of the tubules often enclose a granular deposit which may represent the stained residue of a liquid contained in them during life. The extreme tips of the Malpighian tubules, shown in section in Fig. 6, recall the structure of the anterior excretory portion, since the large granular cell-wall here thins out dorsally to a delicate membrane which closes the end of each of the tubules.

Although the luminous organ of the pupal and imaginal *Bolitophila* has not been studied we may safely assume that it is the same as that of the larva. This is clearly indicated by Hudson's statement that in both the larval and pupal instars it is the last abdominal segment which is luminous, and the fact that at least in Nematoceran Diptera, if we accept the studies of Vaney (1902) on *Simulium* and *Chironomus*, the larval Malpighian tubules are not broken down during metamorphosis but persist with their structure essentially unaltered in the pupa and imago.

The conversion of the distal portion of each of the four Malpighian tubules into a luminous organ in *Bolitophila* is of considerable interest both morphologically and physiologically; morphologically because a single, definite organ is formed by the union or "allelotaxis" of parts of four discrete structures in a manner somewhat analogous to that of the formation of the pituitary body of the Mammalian embryo, and physiologically, because in no other insect are the Malpighian tubules known to have a photogenetic function. Still the assumption of this unusual function does not at present come as a very great surprise, because, though the Malpighian tubules seem to be purely excretory in the great majority of insects, several cases have recently come to light of their acquisition of another function. Thus it has been shown that in larvæ belonging to widely different orders, such as *Chrysopa*, *Myrmeleon* and *Sisyra* among the Neuroptera, and *Lebia* and probably also *Phytonomus* and other Rhynchophora among the Coleoptera, portions of the Malpighian tubules have taken on a secretory function and produce the silk from which the cocoon is spun. The Malpighian tubules of insects are, therefore, functionally more plastic organs than we had supposed and present in this respect a certain analogy to the fat-body, which commonly combines the functions of hæmatopoësis, and the storing of fatty and albuminoid substances and urates. Less frequently, however, the fat-body shows a development of certain of its parts into photogenetic organs (Lampyridæ) and into isolated cells (mycetocytes of Blattidæ) or organ-like cell-aggregates (mycetomata of many Homoptera), which serve as the habitacula of symbiotic Bacteria and Saccharomycetes.

The only other luminous Mycetophilid to which we have been able to find a reference in the literature is *Ceroplatus sesioides*, described many years ago by Wahlberg (1849) from Sweden. The larvæ of this insect live gregariously beneath a glutinous web on the under surfaces of mushrooms (*Polyporus fomentarius*). Wahlberg found the whole body to be luminous in the larval and pupal but not in the imaginal stage. His brief account would seem to indicate that photogenesis in this species, as in certain Chironomidæ, may be due to the presence of phosphorescent Bacteria.

We have endeavored to discover the nature of the food of the larval *Bolitophila luminosa* from examination of the contents of the alimentary tract both in dissections and sections and have found that the creature undoubtedly subsists on insects. The intestine in all the specimens examined was loosely filled with small pieces of chitin, often covered with hairs. Some of the pieces belonged to small gnats allied to the Chironomidæ. In one case a mandible of some small insect larva was found among the fragments. No traces of vegetable matter could be detected. As the head and mouthparts of the larva are extremely small it seems very unlikely that it can seize and dismember active, living prey. It is much more probable that small flying or creeping insects are caught and killed or disabled in the glutinous web and then leisurely devoured by the larva when it comes upon them in its wanderings along the threads. Hudson rejects this supposition on what appears to us to be rather feeble negative evidence. The nature and arrangement of the web certainly indicate that it is used as a trap. He describes it as follows in his second paper (1891): "The web referred to above is suspended in a rocky or earthy niche in the banks of streams in the densest parts of the forest. It consists of a thick glutinous thread stretched across the niche, and supported by several smaller threads running right and left, and attached to the sides and end of the cavity. On this the larva invariably rests, but when disturbed immediately glides back along the main thread, and retreats into a hole which he has provided at the end of it. From the lower side of this central thread numerous smaller threads hang down, and are always covered with little globules of water, resembling a number of minute silver-beaded necklaces, constituting a conspicuous, though apparently unimportant, portion of the insect's web."

That the web must serve as a trap is suggested also by O. F. Cook's recent description (1913) of a similar though more elaborate structure spun by what is in all probability a Mycetophilid larva in the caves of Alta Verapaz, Guatemala. In this case the glutinous web is figured and described as resembling "the rope signals that are hung near bridges and railroad tunnels to avoid accidents to train-crews." Cook found embedded in the slimy threads several small insects such as mosquitoes and other soft-bodied species and even a small beetle, and believes that these constitute the food of the larva.

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EXPLANATION OF PLATE 3.

Abbreviations used: AC, alimentary canal; M, muscle; MT, MT_1, MT_4, portions of Malpighian tubules forming photogenetic organ; OT, point of origin of Malpighian tubules; R, reflector; S, slender, intermediate region of Malphigian tubule; SG, salivary gland; T, trachea.

Fig. 1. Full-grown larva of *Bolitophila luminosa*, from an alcoholic specimen; lateral view.

Fig. 2. Caudal third of body of larva, showing alimentary canal and Malpighian tubules; ventral view.

Fig. 3. Distal portion of Malpighian tubules modified to form photogenetic organ; ventral view.

Fig. 4. Cross-sections through Malpighian tubules; the smaller, upper section from the region S, Fig. 2, the larger, lower one from a region much further forward.

Fig. 5. Section of a piece of the fat-body from the last abdominal segment.

Fig. 6. Cross-section through tips of photogenetic portions of two of the Malpighian tubules.

Fig. 7. Cross-section through the middle of all four of the Malpighian tubules in the photogenetic region. The reflecting layer R is ventral.